STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS

III. GENETIC DIVERSITY IN THE VARIETIES LANDHAFER, SANTA FE, MUTICA UKRAINE, TRISPERNIA AND VICTORIA FOR CROWN RUST RESISTANCE

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Synopsis

Segregation in the F_2 and F_3 generations for rust reaction was studied in certain crosses between members of the group of crown rust resistant varieties comprising Landhafer, Santa Fe, Trispernia, Mutica Ukraine (Ukraine) and Victoria, all resistant to the prevalent Australian races, to assess their genetic diversity with regard to genotypes for resistance. Behaviour in the seedling stage to several races as well as adult plant field reaction was studied. The two factor pairs in Landhafer conditioning adult plant resistance, one of which conferred seedling resistance in addition, were independent of the factors in the varieties Santa Fe, Trispernia and Victoria. The seedling reaction type of Landhafer was epistatic over those of Trispernia and Victoria. The factor for both seedling as well as adult plant resistance in Santa Fe was independent of the factors in Victoria and epistatic to them. Certain modifying gene(s), however, resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was considered allelic with the factors for seedling resistance in the varieties Ukraine and Trispernia, no susceptible segregates occurring within the limits of the population size studied. The factors were not considered identical, however, since Trispernia exhibited a higher reaction type and the allele in Ukraine conditioned resistance to fewer races than that in Santa Fe. The reaction type of Santa Fe was dominant over that of Trispernia in tests with four races, but with race 203 the Santa Fe gene was inhibited by the action of a pair of complementary factors, one contributed by each variety. The three factor pairs in Ukraine, two acting in complementary fashion, involved in adult plant resistance were independent of the Santa Fe gene. Indirect evidence indicated that the factors responsible for seedling resistance in Santa Fe and Victoria were genetically independent. The independence of the factors conditioning adult plant resistance in Landhafer and Ukraine and likewise the independence of the Ukraine and Victoria adult plant factors could not, however, be established in the absence of studies on the appropriate crosses.

Introduction

In a previous paper (Upadhyaya and Baker, 1962*b*) the mode of inheritance in the resistant varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria was reported in the seedling and adult plant stages to certain of the most prevalent field races of crown rust (*Puccinia coronata avenae* Erikss.) in Australia. The relative merits of these varieties in their role in breeding for resistance depend, in addition to the mode of inheritance they exhibit, largely on their diversity with regard to their genotypes for resistance. Information on this latter aspect was obtained from intervarietal crosses between them and is currently presented to show whether the genes which they possess are identical, allelic, or distinct and non-allelic to Australian races.

It also has been pointed out previously that such knowledge is vital to an understanding of the basis and significance of information revealed by physiologic race surveys since these varieties, together with the variety Bond, of which the inheritance will be subsequently reported, form the nucleus of the varieties in the current set used for such surveys.

Literature Review

Results of crosses of the varieties under study with susceptible varieties were reported by Upadhyaya and Baker (1960, 1962*b*). Seedling resistance to various Australian crown rust races was conditioned by a single factor pair in each of the varieties Landhafer, Santa Fe, Mutica Ukraine (Ukraine) and Trispernia, and by four factors, $\underline{Vc_a\ Vc_b}$ (linked complementary) and $\underline{IVc_2\ Vc_2}$ (linked) in the variety Victoria. For adult plant resistance the variety Landhafer possessed an additional recessive factor and Victoria two additional factors $V\bar{c}_1$ and $V\bar{c}_3$. $\underline{IVc_2\ Vc_2}$ were also operative in the adult stage but not $\underline{Vc_a\ Vc_b}$. $V\bar{c}_1$ was linked with $\underline{Vc_a\ Vc_b}$. The factors for seedling resistance in Sant Fe and Trispernia, but not Ukraine, also conditioned adult plant resistance. The adult plant resistance of Ukraine was conditioned by three dominant factors, two acting in complementary fashion.

Several investigators have presented results of studies on crosses between certain or all of the resistant varieties currently being reported. Litzenberger (1949) and Simons and Murphy (1954) found that the factors for resistance in Landhafer and Santa Fe were independent. Finkner (1954) reported that the resistance of Landhafer was genetically independent of those of Santa Fe, Trispernia and Victoria; the factors involved in Ukraine and Victoria were also considered independent. Simons and Murphy (1954) noted complicated inheritance in certain crosses between these varieties. Landhafer × Trispernia gave transgressive segregation with plants more resistant than either parent. A cross between Santa Fe and Trispernia did not indicate allelism between the genes in these varieties.

However, some of the factors found in certain varieties were considered by various investigators to be allelic with, but different from, those in other of the varieties. Finkner (1954) proposed genotypes thus: Ukraine MMUU, Santa Fe $M_1M_1U_1U_1$ (or M_1M_1) and Trispernia M_2M_2 and/or two other factors. Both factors in Ukraine were dominant over those with which they were allelic in Santa Fe; similarly M_1 was dominant to M_2. Finkner, Atkins and Murphy (1955) reported that one (M_1) of the two linked genes in Santa Fe was allelic with the single gene M in Ukraine, and recessive to it.

With race 57 of the pathogen, and representing the single genes found to condition resistance in Landhafer and Victoria as L and V respectively, Finkner (1954) concluded that the allelic and non-allelic relationships with regard to dominance or epistasis were in the following order: M or $U > M_1$ or U_1 or $L > V > M_2$. The immune reaction of Ukraine was dominant or epistatic to that in the other varieties.

Materials and Methods

F_1, F_2 and F_3 generations were studied for crown rust reactions in crosses between the five varieties under study. The following crosses were not included because either the cross was not made or the F_1s failed to set seed due to adverse environmental conditions: Ukraine × Landhafer, Ukraine × Trispernia, Ukraine × Victoria and Trispernia × Victoria.

Crown rust races employed for testing were 203, 226, 237, 237–4, 259 and 286. These are described by Baker and Upadhyaya (1955) and were built up from field isolates.

The experimental procedures were set out by Upadhyaya and Baker (1960).

Experimental Results

F_1 reaction types

The reaction types in the F_1 of the various crosses in the seedling and also the adult plant stages, together with those of the parents to different specific races as well as field inoculum, are presented in Table 1.

Genes conditioning resistance in certain of these varieties will be suggested below to be allelic. In these cases the F_1 behaviour was an indication of the dominance relationship. In cases of non-allelism the degree and type of epistasis manifest was evident from the F_1 behaviour. From the data in Table 1 in

TABLE 1

Reaction types in the seedling stage and reactions in the adult plant stage of the parents and F_1s in certain oat crosses to specific races or field inoculum of Crown Rust

Parental Varieties or Cross.	Reaction types in seedling stage Race 203	237	237–4	226	259	286	Reactions in adult plant stage Race 203	237	237–4	226	259	Field inoculum.
Landhafer and Santa Fe[1]	; — 1 =	; — 1 =	; — 1 =	; — 1 =	; — 1 =	4	I	I	I	I	I	I
Ukraine[1]	4	; — 1 =	; — ; =	4	4	4	R	I	I	I	R—MR	I, R—MR
Trispernia	1+	1+	1+	1+	1+	4	—	—	—	—	—	R
Victoria	1n	1n	1n	1n	3	1n	R	R	R	I	S	I(98%)
Landhafer × Santa Fe	; — 1	;	;	;	; — 1	—	I	I	I	I	I	I
Landhafer × Trispernia	—	—	—	—	1	—	—	—	—	—	—	R
Landhafer × Victoria	; — 1	1cn	1cn	;	1 — 1+	1n — 2–n	—	R	—	I	R—MS	R
Santa Fe × Ukraine	—	;	; , 1 =[1]	—	;	—	R	R	R	R	R	—
Santa Fe × Trispernia[1]	—	—	—	3–c	2	—	—	—	—	—	—	I
Santa Fe × Victoria	—	—	—	—	1+, 2++	1n — 2–n	—	—	—	—	—	I

[1] Reactions observed at temperatures above 80°F.
I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

TABLE 2

F_2 seedling segregation for reaction type in crosses involving the oat variety Landhafer to certain races of Crown Rust to which both parents were resistant

Cross.	Race used	F_2 Reaction types						Expected ratio	P value
		; (R)	1 (SR)	2– (In)	3–4 (S)	Total			
Santa Fe × Landhafer	226[1]	119	69	1	18	207		11R : 4SR : 1S	<0·01
					(12·9)			15(R+SR) : 1S	0·2–0·1
	203	122	18	1	13	154		11R : 4SR : 1S	0·2–0·1
					(9·6)			15(R+SR) : 1S	0·3–0·2
	237–4[1]	190	102	1	28	321		11R : 4SR : 1S	<0·001
					(20·1)			15(R+SR) : 1S	0·1–0·05
	259	255	92	5	29	381		11R : 4SR : 1S	0·7–0·5
					(23·9)			15(R+SR) : 1S	0·7–0·5
	Total	686	289		88 (66·4)	1063		15(R+SR) : 1S	0·02–0·01
		; (R)	1+(SR)	(2–3c) (In)	3–4(S)				
Landhafer × Trispernia	259[2]	101	188	58	27 (23·4)	374		4R : 9SR : 2In : 1S	0·1–0·05
		; (R)	1+(SR)	In(SR)	2–n (In)	(3–4) S	Total		
Victoria × Landhafer	203	73	102	37	7	15	234	75(R+SR)[4] : 18(SR+In)[5] : 7S	0·95–0·9
		(174·8)		(41·9)		(16·3)			
	226	96	9	18	1	8	132		0·5–0·3
		(99·0)		(23·8)		(9·2)			
	237[2]	43	64	26	3	12	148		0·8–0·7
		(111·0)		(26·6)		(10·4)			
	Total	387 (384·8)		91 (92·3)		35 (35·9)	513		0·99–0·95
	237–4[3]	— (35·8)	32	101 (97·2)		10 (10·0)	143	25(R+SR)[4] : 68(R+SR)[5] : 7S	0·8–0·7

[1] Identical plants tested first to race 237–4 and then to race 226.
[2] Reaction types corrected from F_3 behaviour.
[3] Reaction types recorded at temperatures of about 80°F.
[4] R and SR reactions due to homozygosity or heterozygosity of Landhafer genotype.
[5] R and SR reactions due to homozygosity or heterozygosity of Victoria genotype.
(Expected values in brackets).
R = Resistant, SR = Semi-resistant, In = Intermediate, S = Susceptible.

certain cases the lower reaction type (higher resistance) was either completely dominant or epistatic or the F_1 reaction type was intermediate between the parental types. In tests against races 259 and 286, Victoria being susceptible to the former and Landhafer and Santa Fe susceptible to the latter race, the F_1s of crosses of Victoria with Landhafer and Santa Fe showed intermediate reaction types. In other cases F_1 reaction types slightly or distinctly less resistant than either parent were observed. This occurred in the crosses Landhafer × Santa Fe, Santa Fe × Ukraine and Santa Fe × Trispernia tested with certain races.

F_2 segregation

(i) Seedling tests

The results of studies at the seedling stage on F_2 populations of crosses tested with one or several different races to which both parents were resistant are presented in Tables 2 and 3. Table 2 pertains to crosses involving the variety Landhafer.

In the cross Santa Fe × Landhafer the presence of approximately one susceptible plant in 16 in all tests suggested that the single factor pairs for resistance in both these varieties revealed in their crosses with susceptible varieties were genetically independent. Thus 7/16 of the population were expected to be resistant similar to the parents giving a " ; " to " 1= " reaction type, and one-quarter semi-resistant resulting from the heterozygous effect of each incompletely dominant gene singly. Doubly heterozygous plants on this hypothesis would comprise one quarter of the F_2 population and their reaction type might be expected to be resistant corresponding to that shown by the F_1 seedlings which varied from " ; " to " 1—1n " according to particular tests. However, when tested to this predicted 11 resistant : four semi-resistant : one susceptible seedling ratio in the F_2 generation it was obvious that in two out of the four cases the number of semi-resistant plants was considerably in excess of that calculated, indicating that some of the doubly heterozygous class had a higher reaction than that predicted, due probably either to environmental effects or to the segregation and action of modifying genetic factors.

In this cross also, whilst individual tests showed good agreement with the predicted 15 (resistant + semi-resistant) : one susceptible F_2 seedling, there was a small, though not statistically significant, excess number of susceptible plants in all cases and, due to this, the total of all tests did not show a good fit to a dihybrid 15 : 1 ratio, the P value being $0 \cdot 02 - 0 \cdot 01$. It is difficult to explain this result since, if any linkage were envisaged between the genes in Landhafer and Santa Fe, they would be expected to be present in the repulsion phase, resulting in a deficiency rather than an excess of susceptible plants. In this cross a few F_2 seedlings of an intermediate (" 2— ") reaction type were observed and for statistical tests these were grouped with the semi-resistant class.

In F_2 segregates of the cross Landhafer × Trispernia, the factor pair in Trispernia, in the absence of that in Landhafer, in the heterozygous condition was expected to show an intermediate reaction type varying from " 2 " to " 3c " from the behaviour of Trispernia in crosses with susceptible varieties ; only those seedlings homozygous for the Landhafer factor pair were expected to give a resistant (" ; ") reaction type. Thus the expected F_2 ratio was four resistant : nine semi-resistant : two intermediate : one susceptible plant. The deviations were not significant at the five per cent level. However, by grouping the two middle classes and comparing with a four resistant : 11 intermediate : one susceptible plant ratio, a better fit was obtained statistically, the P value being $0 \cdot 5 - 0 \cdot 3$ compared with $0 \cdot 1 - 0 \cdot 05$.

Since in the cross Landhafer × Victoria the F_1 behaviour showed epistasis or partial epistasis of the Landhafer reaction type, according to the particular race employed, three-quarters of the F_2 seedlings in this cross were expected to show the homozygous or heterozygous reaction type of the Landhafer gene similar to that in its crosses with susceptible varieties. One-quarter would therefore be expected to show a " ; " to " 1= " reaction type and one-half a " 1 " reaction type or one approximating this at normal temperatures (below 75° F). The remaining 25 per cent was expected to show segregation for the Victoria type crown rust resistance in the ratio of 71·9 per cent resistant (" 1n " to " 2 " reaction types) : 28·1 per cent susceptible (Upadhyaya and Baker, 1960). Due to the presence of the large number of segregating factors involved in the cross, the distinction between the " ; 1= " and " ; 1 " reaction types was not clear cut and the two classes were combined for statistical calculations. Hence the expected F_2 ratio in this cross was 75 per cent " ; " to " 1 " reaction types (due to Landhafer), 18 per cent " 1n " to " 2 " (due to Victoria), and seven per cent susceptible. Results with three races separately and the combined total agreed well with this hypothesis. The tests involving race 237–4 were conducted at temperatures between 75° and 85° F. At these temperatures it was observed previously that the Landhafer factor alone in the heterozygous condition gave plants of an intermediate (" 2 " to " 3 —c ") reaction type. In this instance the expected ratio was 25 per cent resistant (" ; " to " 1 " reaction types) : 68 per cent intermediate (" 2 — " to " 3c " reaction types) : seven per cent fully susceptible, and the observed results agreed satisfactorily with this hypothesis.

In the cross Santa Fe × Ukraine 570 and 147 seedlings respectively were tested to races 237–4 and 237 and no susceptible segregates were observed, indicating that the single factor pairs in each case were allelomorphic or closely linked. Although to races to which both were resistant the reaction type was very similar in both varieties, the factors were not identical since that in Ukraine conditioned resistance to fewer races. It has been shown previously that the resistance of Santa Fe to a large number of races to which it is resistant is due to the same factor pair (Upadhyaya and Baker, 1962*b*).

Results involving F_2 seedling segregation in crosses of Santa Fe with Trispernia and Victoria are presented in Table 3. In the total F_2 population of 840 seedlings involving tests with four races, no susceptible segregates were observed in the cross Santa Fe × Trispernia. In tests involving race 259, 13 plants were noted with a slightly higher reaction type than Trispernia but this may have been due to segregation of modifying genes or to high temperature effects on reaction type. The absence of susceptible segregates in F_2 indicated that the factors in Santa Fe and Trispernia were allelic or closely linked. The genes were considered to be distinct in view of the consistently higher reaction type of Trispernia. Hence the single factor pairs in each of the three varieties Santa Fe, Ukraine and Trispernia conditioning seedling resistance were considered to constitute an allelic series.

Since F_1 seedlings in the cross Santa Fe × Victoria were tested only with races 259 and 286, to neither of which were both parents resistant, no evidence was available on epistastis of reaction types. However, following the observations on a Victoria × Landhafer cross where the Victoria reaction type with characteristic necrosis was hypostatic, the hypothesis of 25 per cent Santa Fe reaction types, 50 per cent intermediate between Santa Fe and Victoria (resistant reaction types with no necrosis), 18 per cent Victoria reaction types (resistant with necrosis) and seven per cent susceptible segregates in F_2 was adopted. On this hypothesis only in tests involving race 237–4 was a good statistical fit obtained. In the other two tests the number of Santa Fe types was too few and the Victoria reaction types in excess of that expected. A satisfactory statistical fit was obtained in these cases only when the resistant classes of reactions were grouped and the hypothesis of 93 resistant : seven susceptible F_2 plants adopted. This suggested that the Santa Fe reaction type was not completely epistatic to that in Victoria or that segregating modifying genes from one or both parents were operative.

TABLE 3

F_2 seedling segregation for Crown Rust reaction type in crosses involving the oat variety Santa Fe with the varieties Trispernia and Victoria, to races to which both parents were resistant

Cross.	Race used	F_2 Reaction types ;	1 = , 1	1+ , 2–	2	3–4	Total	Expected ratio	P value
Santa Fe × Trispernia ..	226[2]	175	—	50 (56·3)	—	—	225	3(;) : 1(1+ , 2–)	0·5–0·3
	230[2]	65	—	22 (21·8)	—	—	87	do.	0·99–0·95
	237–4[1]	36	— 84 (90·0)	—	—	—	120	1(;) : 3(other reaction types)	0·3–0·2
	259[3]	147	129	119	13	—	408	do.	<0·001
		(102·0)	(306·0)						
		;	1 = , 1	1n	2–n	3–4			
Santa Fe × Victoria ..	203	100	230	145	13	31 (36·3)	519	(*a*) 25(;) : 50(1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	<0·001 0·5–0·3
	226[2]	112	24	56	15	17 (15·7)	224	(*a*) 75(; & 1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	<0·001 0·8–0·7
	237–4	20 (27·0)	64 (54·0)	16 (19·4)	—	8 (7·6)	108	(*a*) 25(;) : 50(1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	0·3–0·2 0·9–0·8

[1] Plants with ' ; ' reaction types only separated out.
[2] Reactions recorded in temperature controlled room (65 ± 2°F).
[3] Reactions read at normal temperatures in glasshouse.
(Expected values in brackets.)
R = Resistant (reaction type 2 or lower), S = Susceptible.

(ii) Adult plant tests

Results of F_2 segregation in the adult plant stage under field conditions are presented in Table 4.

It was shown in a previous paper (Upadhyaya and Baker, 1962*b*) from data on the cross Burke × Landhafer that, under field conditions, Landhafer possessed an additional factor (recessive in action) for crown rust resistance operative in the adult plant stage only. With the operation of three independent factor pairs conditioning adult plant resistance (one recessive in action) in crosses involving Landhafer with Santa Fe or Trispernia, a ratio of 61 resistant : three susceptible plants was expected for F_2 field segregation. In the cross Santa Fe × Ukraine the expected ratio was 249 resistant : seven susceptible with four factors involved (three from Ukraine, two acting in dominant complementary fashion and one from Santa Fe). No susceptible segregates were expected in F_2 in the cross Santa Fe × Ukraine since the same factors conditioned both seedling and adult plant resistances in each case and the seedling resistances were previously indicated to be allelic (or closely linked). The segregations in crosses involving the variety Victoria were based upon the presence of four factor pairs in this variety, Vc_2Vc_2 and IVc_2IVc_2 linked with ten per cent recombination, and two independent factor pairs, $V\bar{c}_1Vc_1$ and $V\bar{c}_3Vc_3$ giving in crosses with susceptible varieties 5·95 per cent susceptible adult plants (Upadhyaya and Baker, 1960). With the two factors for adult plant resistance contributed by Landhafer the percentage of susceptible F_2 plants would be expected to be 1·12 in the cross Victoria × Landhafer.

Table 4

F_2 segregation for adult plant field reaction to Crown Rust in certain crosses involving the resistant oat varieties Landhafer and Santa Fe with other resistant varieties

Cross	Adult plant field reactions				Total	Expected ratio	P value
	I	R	MR	MS–S			
Santa Fe × Landhafer ..	343	96	10	23 (22·1)	472	61 : 3	0·9–0·8
Landhafer × Trispernia ..	184	50	19	16 (11·7)	249	61 : 3	0·3–0·2
Victoria × Landhafer ..	201	3	—	2 (2·3)	206	98·88 : 1·12	0·9–0·8
Santa Fe × Victoria	207	9	28	14 (15·4)	258	94·05 : 5·95	0·8–0·7
Santa Fe × Ukraine	56	6	5	2 (1·5)	69	249 : 7	0·7–0·5
Santa Fe × Trispernia[1] ..		– 453 –		0	453	all R	—

[1] No separate classification for the different types of resistance carried out

(Expected values in brackets.)

I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

In all the above cases in F_2 adult plant segregation good agreement statistically between observed and expected results was observed on the basis of these hypotheses presented. In the cross Santa Fe × Victoria the percentage of susceptible plants would be expected to be 1·49 with the four factors from Victoria and one from Santa Fe. Hence in the 258 plants tested, approximately four susceptible plants would have been expected. This deviates markedly from the 14 observed. The results in the cases of this cross were best explained on the operation of only one of the two factors ($\bar{Vc_1}$ or $\bar{Vc_3}$) conditioning adult plant resistance in Victoria, on which basis 15·4 susceptible plants would have been expected.

These results confirmed the operation of the following factors conditioning adult plant resistance to crown rust: Two factors in Landhafer (one recessive in inheritance).—One factor each in Santa Fe and Trispernia, the factors being allelic and identical with those conferring seedling resistance.—Three factors in Ukraine, two acting in complementary dominant fashion.—One factor in Victoria linked with a dominant inhibitor gene and one or two additional adult plant factors according to the particular cross involved.

F_3 segregation

Seedling tests of F_3 progenies from seedling classified F_2 plants were conducted by taking representative samples from the major F_2 reaction categories. The expected F_3 behaviour in the various crosses was as follows:

Cross	F_3 behaviour		
	Resistant	Segregating	Susceptible
Santa Fe × Landhafer	7	8	1
Landhafer × Trispernia	7	8	1
Santa Fe × Trispernia	All resistant		
Santa Fe × Ukraine	All resistant		
Victoria × Landhafer Victoria × Santa Fe	40·4%	52·6%	7·0%

These expectancies could be further categorized and subdivided in certain cases thus:

Landhafer × Trispernia

Resistant 7, comprising four homozygous for the partially epistatic Landhafer resistance ("1=" reaction type) denoted by Ld, one homozygous for Trispernia resistance ("1+" reaction type) denoted by Tr, and two segregating for Landhafer and Trispernia reaction types (denoted by Ld : Tr), the hypostatic Trispernia gene appearing due to the heterozygous state of the Landhafer gene in this particular genotype.

Segregating 8, comprising four segregating for the Landhafer reaction type (preponderant), Trispernia reaction type and susceptible plants, two segregating for Landhafer reaction type and susceptibility, the designation Ld (Tr) : S being used to represent both categories, and two segregating for Trispernia reaction type and susceptibility (designated Tr : S).

Santa Fe × Trispernia

All resistant, comprising one homozygous for the Santa Fe resistance (";" to "1=" reaction type), two segregating for the Santa Fe and Trispernia resistances ("1+" reaction type), designated as S.F. : Tr, and one homozygous for Trispernia resistance.

Victoria × Landhafer

Resistant 40·4 per cent, comprising 25·0 per cent homozygous for the epistatic Landhafer resistance (denoted by Ld), 10·3 per cent segregating for the Landhafer and Victoria reaction types (symbolized as Ld : Vc), and 5·1 per cent homozygous for the Victoria resistance (denoted by Vc).

Segregating 52·6 per cent, comprising 39·8 per cent segregating for Landhafer resistance and susceptibility, or Landhafer and Victoria resistances and susceptibility (designated as Ld (Vc) : S), and 12·8 per cent segregating for Victoria reaction type and susceptibility (denoted as Vc : S).

Susceptible 7·0 per cent, comprising those segregating for susceptibility and a low proportion of Victoria type resistant plants (symbolized as S : Vc) and those lines homozygous susceptible (denoted as S).

Victoria × Santa Fe

Similar categories to those in the Victoria × Landhafer cross.

In the cross Santa Fe × Ukraine no segregation was noted in tests involving a mixture of races 237 and 237–4. Table 5 presents the F_3 data relevant to Santa Fe in crosses with Landhafer and Trispernia and shows good agreement between observed and expected results.

Table 5

Seedling behaviour of F_3 lines in crosses involving the resistant oat variety Santa Fe with the resistant varieties Landhafer and Trispernia tested with Race 203 of Crown Rust

Cross	F_3 Behaviour			Total	P value
	Res.	Seg.	Sus.		
Santa Fe × Landhafer	105 (110·3) Homo.S.F.	131 (126·0) Seg.S.F. : Tr.	16 (15·8)[1] Homo.Tr.	252	0·9–0·8
Santa Fe × Trispernia	28 (26·8)	51 (53·5)	28 (26·8)[2]	107	0·9–0·8

[1] = Expected ratio 7 : 8 : 1 resp.
[2] = Expected ratio 1 : 2 : 1 resp.
Res. = Resistant, Seg. = Segregating, Sus. = Susceptible. Homo. S.F. = Homozygous for Santa Fe reaction type (;). Seg. S.F. : Tr. = Segregating for Santa Fe reaction type (;) and Trispernia reaction type (1+). Homo. Tr. = Homozygous for Trispernia reaction type (1+).
(Expected values in brackets).

Data involving the three other crosses studied, Landhafer × Trispernia and Victoria in its crosses with Landhafer and Santa Fe, are presented in Table 6. Comparison of expected and observed results within the previously indicated subclasses of two of the three F_3 categories, viz. homozygous resistant and segregating, in these crosses are included in this table. There was good statistical agreement between observed and expected results, except in the cross Santa Fe × Victoria where the agreement was satisfactory only when the major classes (resistant, segregating and susceptible) were considered but not further subdivided.

When the F_2 classification for reaction types was based on F_3 breeding behaviour in the three crosses, 75 per cent would be expected to be Landhafer or Santa Fe types, 18·75 per cent Trispernia or 18 per cent Victoria types, and the remainder susceptible. From F_3 data the appropriate factors were separated as follows where the observed and expected numbers (in brackets) are compared :

	Ld. or S.F. types	Tr. or Vc. types	Susceptible
Landhafer × Trispernia	135(136·5)	34(34·2)	13(11·3)
Victoria × Landhafer	63(62·3)	15(14·8)	5(5·8)
Santa Fe × Victoria	293(320·0)	104(76·2)	29(29·8)

TABLE 6

Seedling behaviour of F_3 lines in the crosses Landhafer × Trispernia, Victoria × Landhafer and Santa Fe × Victoria tested with races to which both parents were resistant

F_3 behaviour	Landhafer × Trispernia Race 226				Victoria × Landhafer Race 203				Santa Fe × Victoria Races 226 and 237			
	Exp. ratio	Reaction type(s)	Obs.	Exp.	Exp. ratio	Reaction type(s)	Obs.	Exp.	Exp. ratio	Reaction type(s)	Obs.	Exp.
Resistant	4	Ld.(1 =)	48	45·5	25·0	Ld.(1 =)	25	20·8	25·0	S.F.(1 =)	78	106·5
	2	Seg. Ld.(1 =) & Tr.(1+)	21	22·8	10·3	Seg. Ld.(1 =) & Vc.(1n)	11	8·6	10·3	Seg. S.F.(1 =) & Vc.(1n)	54	43·9
	1	Tr.(1+)	8	11·4	5·1	Vc.(1n)	4	4·2	5·1	Vc.(1n)	37	21·7
Segregating ..	6	Seg. Ld.(1 =), Tr.[1] (1+) & S(4)	66	68·3	39·8	Seg. Ld.(1 =), Vc.[1] (1n) & S(4)	27	33·0	39·8	Seg. S.F.(1 =), Vc.[1] (1n) & S(4)	161	169·6
	2	Seg. Tr.(1+) & S(4)	26	22·8	12·8	Seg. Vc.(1n) & S(4)	11	10·6	12·8	Seg. S.F.(1 =) & S(4)	67	54·5
Susceptible ..	1	S(4)	13	11·4	7·0	S(4)	5	5·8	7·0	S(4)	29	29·8
Total	16		182	182·2	100·0		83	83·0	100·0		426	426·0
			$\chi^2 = 2·04$ P = 0·9–0·8				$\chi^2 = 2·81$ P = 0·8–0·7				$\chi^2 = 23·99$ P < ·001 major classes (Res., Seg., Sus.) $\chi^2 = 0·15$ P = 0·95–0·9	

[1] These reaction types would be expected to be absent in certain lines.
Ld. = Homozygous for Landhafer reaction type (1 =) ; Tr. = Homozygous for Trispernia reaction type (1+) ; Vc. = Homozygous for Victoria reaction type (1n) ; S.F. = Homozygous for Santa Fe reaction type (1 =) ; S = Homozygous susceptible reaction type (4). Res. = Resistant, Seg. = Segregating, Sus. = Susceptible.

The observed frequencies in the first two crosses showed no significant deviations from those expected. In the cross Santa Fe × Victoria, however, it was clear that an excessively large number of lines showed the Victoria reaction type on the hypothesis adopted. Reference has already been made to similar conclusions based on F_2 data. Unfortunately, as previously indicated, no studies of F_1 reaction type where epistasis could be directly assessed were carried out in this cross in tests involving races to which both parents were resistant. The greater number of F_2 plants and of F_3 lines showing the Santa Fe type of resistance suggested the epistatic behaviour of the Santa Fe reaction type over that of Victoria. The general observation in all crosses in general, that the lower reaction type was epistatic, supports this hypothesis. Certain genotypes, however, involving the variety Victoria, seemed to have inhibited the action of the Santa Fe gene. Such behaviour was evident in studies on correlated tests of identical F_3 lines involving race 226 (to which both parents were resistant) and race 286 (to which only Victoria was resistant). The data are included in Table 12.

Relationship of seedling reaction types to different races and to adult plant field reactions

(i) F_2 seedling vs. F_2 seedling

This correlation was studied only in the cross Landhafer × Santa Fe, where 321 F_2 plants were first classified for primary leaf reaction type to race 237 and the leaves subsequently cut off and of these 207 were then inoculated at the secondary leaf stage with race 226. Perfect correlation of reaction types was observed in this test.

(ii) F_2 seedling vs. F_2 adult plant

This association was studied in all crosses except Victoria × Landhafer. Classified seedlings were transplanted and tested in the field for subsequent adult plant behaviour. The resistant class was expected to maintain its resistance at the adult plant stage in Landhafer crosses but, due to the operation of an additional factor conditioning adult plant resistance in this variety, the seedling susceptible class was expected to produce some resistant adult plants. In the cross Santa Fe × Landhafer, 86 seedlings tested maintained their resistance; in the cross Landhafer × Trispernia only one plant giving an intermediate type of reaction for the heterozygous condition of the Trispernia gene gave a susceptible field reaction, the other 193 seedlings maintaining their resistance as adult plants. In the susceptible class one plant out of nine in the former cross and five out of thirteen in the latter cross remained fully susceptible, the segregation thereby conforming within approved statistical limits to the expected 3 resistant : 1 susceptible ratio. These resistant adult plants, in both cases from the susceptible seedling group, varied in reaction type, one being immune, six resistant, and one moderately resistant in the cross Santa Fe × Landhafer, the corresponding figures in the cross Landhafer × Trispernia being three, four and one, thus showing that the factor conditioning only adult plant resistance in Landhafer was incompletely dominant in inheritance.

Since the single factor pairs conditioning seedling as well as adult plant resistance in both Santa Fe and Trispernia were previously shown to be allelic (or closely linked) in the seedling stage, no susceptible F_2 adult plant segregates were expected in the cross between these two varieties; none were observed among 192 plants tested.

In tests involving race 226 (to which Ukraine was susceptible) seedling resistant F_2 plants in the cross Santa Fe × Ukraine were expected to remain resistant as adult plants due to the influence of the Santa Fe gene, and susceptible seedlings were expected to show a 57 resistant : 7 susceptible adult plant segregation due to the action of the three factors (two acting in complementary fashion) conditioning adult plant resistance in Ukraine. In the cross Victoria × Santa Fe in tests involving races to which both parents were resistant, seedlings possessing the Santa Fe reaction type (" ; " to " 1= ") were expected to remain resistant as adult plants. The group of seedlings possessing the Victoria reaction type (" 1n ") and those susceptible were expected to show some susceptible and resistant adult plants respectively. Previously cited F_2 data indicated that in this cross only one factor conditioning solely adult plant resistance in Victoria was operative. This factor, when linked with two complementary factors for seedling resistance, was expected to show the following relationship between seedling and adult plant behaviour in F_2:

Adult plant reactions	Seedling reaction types		
	Santa Fe type	Victoria type	Susceptible
Immune—Moderately resistant	100%	66·9%	9·5%
Moderately susceptible —Susceptible ..	—	5·0%	18·6%

Data relating to crosses of Santa Fe with Ukraine and Victoria are presented in Table 7. In all cases good statistical fits to the expected results were clearly obtained and confirmed the operation of three factors in Ukraine and one major factor in Victoria for adult plant resistance.

TABLE 7

Relationship between seedling reaction types and adult plant reactions to Crown Rust of F_2 plants in crosses of the oat variety Santa Fe with the varieties Ukraine and Victoria

Adult plant reactions	Seedling reaction types (Race 226)[1]							
	Santa Fe × Ukraine			Santa Fe × Victoria				
	;	1=, 1	3–4	;	1=, 1	1n	2–n	3–4
Immune	59	7	—	34	15	27	—	1
Resistant	5	3	3	—	—	2	—	3
Mod. Res.	3	2	11	—	—	—	11	—
Total	67	12	14	34	15	29	11	4
			(12·7)			(35·5)		(5·0)
Mod. Sus. and Susceptible	—	—	1	—	—	—	1	8
			(2·3)			(2·6)		(9·9)
P value			0·7–0·5[2]				0·7–0·5	

[1] Seedling reaction types corrected from F_3 behaviour.
[2] Yates' correction factor applied for small numbers.
Mod. Res. = Moderately resistant, Mod. Sus. = Moderately susceptible.
(Expected values in brackets.)

(iii) F_2 seedling vs. F_3 seedling

The F_3 behaviour of representative samples from each F_2 class of reaction type was studied in all crosses except Santa Fe × Ukraine. In certain cases the particular race to which the F_2 was tested was used in a mixture with certain other races for F_3 tests. In other cases, a mixture not involving the particular race used in F_2 was utilized, whilst in one test an identical strain (race 226) was used in tests for both generations. The data pertinent to these studies are set out in Table 8 and were designed to study the postulated breeding behaviour of F_2 genotypes based on reaction types and to investigate if the same factors were operative against all races.

In the cross Santa Fe × Landhafer one plant each from the highly resistant class (" ; " reaction type) and moderately resistant class (" 2 – " reaction type) of F_2 segregates gave susceptible progenies. The latter plant would have been expected to be heterozygous on reaction type and hence segregate in F_3. Classification as homozygous susceptible may have been erroneous, due to the chance absence of a resistant plant, but this would be highly improbable statistically in the sample of approximately 25 plants tested in each F_3 line. One moderately resistant F_2 plant (" 2 -- " reaction type) also gave a homozygous susceptible line, but this could occur statistically at a relatively high probability level as pointed out by Upadhyaya and Baker (1962*a*). Except for these instances, the first of which was almost certainly due to an error in classification, labelling or transplanting, all other plants from the different F_2 reaction classes behaved as expected, indicating correlated inheritance to all races with which they were tested, since no mixed reaction types were observed on the same leaf by the use of inoculum comprising a mixture of races.

In the cross Santa Fe × Trispernia there was also good agreement between observed and expected results. The operation of certain modifying genes was indicated, however, since from the " 1 " reaction type in F_2, 12 plants gave homozygous highly resistant progenies similar to Santa Fe (" ; " to " 1= " reaction type). In the F_2 classification also certain seedlings had shown reaction types higher than Trispernia ; the progenies of these plants showed reaction types similar to Trispernia at normal temperatures of about 75°F, except for one plant which showed segregation for the Santa Fe and Trispernia reaction types.

In the cross Victoria × Landhafer also good agreement between the F_2 reactions to race 237 and F_3 behaviour to a mixture of races 226, 237 and 237–4 was shown. Only four lines—one homozygous resistant for the Victoria reaction type and three segregating for Victoria type resistance and susceptibility —were observed from F_2 plants in the " 1 – " to " 1 " reaction type category intermediate between that of Landhafer and Victoria and expected to segregate for the Landhafer reaction type and susceptibility. This discrepancy may have been due to difficulty in distinguishing the necrotic reaction type associated with the Victoria type of resistance on the basis of a single F_2 plant. Similarly, a small number of discrepancies were observed in the cross Landhafer × Trispernia. The difficulty in distinguishing a " 2 " reaction type with the associated " green island " from a " 3 " type with the pustule surrounded by chlorosis resulted in three plants assigned to the former class giving homozygous susceptible progenies and two to the latter class producing segregating progenies. Apart from these instances it was clear that the same factors in the two varieties conditioned resistance to the four races 226, 237, 237–4 and 259.

In the cross Santa Fe × Victoria, F_2 plants classified for reaction type to race 203 were tested for their progeny reactions against races 226 and 237 separately. Reactions in F_3 were corrected, taking into account behaviour to both races since small numbers of seedlings were tested to each race separately. For example, if an F_3 line was apparently homozygous resistant to one race in the small sample tested, but segregating to the other, its behaviour was indicated as segregating. In another test, F_2 and F_3 reaction types were noted when both were tested against the same race—race 226. Agreement between observed and expected results was not completely satisfactory in this cross and discrepancies existed in certain instances. From among the 85 F_2 plants classified as possessing the Santa Fe reaction type (" ; "), three were found to

TABLE 8

F_3 behaviour of F_2 plants classified for seedling reaction type to Crown Rust in crosses involving the resistant oat varieties Landhafer and Santa Fe

F_2 Reaction types of various crosses to different races		F_3 reactions to race(s)						Total
		226, 237, 237–4 and 259						
Race 259		Res.	Seg.	Sus.				
Santa Fe × Landhafer	;	35	18	1				54
	1	1	23	—				24
	2–	—	3	1				4
	3–4	—	—	7				7
		226, 237, 237–4 and 259						
		S.F.[1]	S.F. : Tr.[2]	Tr.				
Santa Fe × Trispernia	;	13	12	—				25
	1	12	36	2				50
	2–	—	6	20				26
	2	—	1	5				6
		Ld.	Ld. : Tr.	Tr.	Ld.(Tr.) : S.	Tr.: S.	S.	
Landhafer × Trispernia	;	46	13	—	11	—	—	70
	1–2=	1	7	1	46	1	—	56
	2–	—	4	2	6	3	—	15
	2	—	—	2	3	21	3	29
	3–4	—	—	—	—	2	12	14
Race 237		226, 237 and 237–4						
		Ld.	Ld. : Vc.	Vc.	Ld.(Vc.) : S.	Vc. : S.	S.	
Victoria × Landhafer	;	3	1	—	3	—	—	7
	1– –1	—	1	1	8	3	—	13
	1n – 2–n	—	—	4	—	4	—	8
	3n	—	—	—	—	3	—	3
	3–4	—	—	—	—	—	7(2 S. : Vc.)	7
Race 203		226 and 237						
		S.F.	S.F. : Vc.	Vc.	S.F.(Vc.):S.	Vc.:S.	S.	
Santa Fe × Victoria	;	32	10	1	2	1	—	46
	1	11	7	2	43	—	—	63
	1+, 3–c	—	—	—	15	2	—	17
	1n, 2–n	—	6	19	19	26	—	70
	2n, 3n	—	—	1	2	8	—	11
	3–4	—	—	—	—	1	16(8 S.Vc.)	17
Race 226			226					
	;	11	9	2	14	2	1	39
	1	—	2	—	13	—	—	15
	1n– 2–n	—	—	5	—	20	—	25
	2n– 3n	—	—	2	1	4	1	8
	3–4	—	—	—	—	1	10(3 S. : Vc.)	11

Reaction types indicated as follows :—S.F. = Homozygous ; – 1 = ; Tr. = Homozygous 1+ ; Ld. = Homozygous ; – 1 = ; Vc. = Homozygous 1n ; S. = Homozygous 3-4 reaction types ; S.F. : Tr., etc. = segregating for S.F. and Tr. reaction types etc. ; Ld. (Tr.) : S., etc. = segregating for Ld. reaction type and susceptibility or Ld. and Tr. reaction types and susceptibility, etc. ; S. : Vc. = segregating for Vc. reaction type and susceptibility with preponderance of susceptible plants ; Res. = Homozygous resistant ; Seg. = Segregating ; Sus. = Homozygous susceptible.

be homozygous for the Victoria reaction type (" 1n "), three segregated for this reaction type and susceptibility, and one was homozygous for susceptibility. Of 78 plants classified as showing a " 1 " reaction type, intermediate between Santa Fe and Victoria, two were homozygous for the Victoria type of resistance, whilst two segregated for the Victoria reaction type. A total of 28 plants from

TABLE 9

F_3 seedling behaviour to certain Crown Rust races of F_2 plants classified for adult plant reaction in crosses involving the resistant oat varieties Landhafer and Santa Fe

Cross	F_2 Field reaction	F_3 Seedling behaviour or reaction type(s) Res.	Seg.	Sus.	Total	P value
		Races 226, 237, 237–4 and 259				
Santa Fe × Landhafer	I	44	42	—	86	
	R	1	41	—	42	
	MR	—	7	3	10	
	MS–S	—	4	8	12	
		Races 226 and 226–2				
Santa Fe × Ukraine	I	14	26	7	47	
	R	1	3	2	6	
	MR	—	1	4	5	
	Total	15(14·8)	30(29·9)	13(13·3)	58	0·9–0·8
	MS–S	—	—	2(2·0)	2	—

Cross	F_2 Field reaction	S.F.	S.F.:Vc.	S.F.(Vc.):S.	V.c	Vc.:S.	S.	Total
		Race 226						
Santa Fe × Victoria	I	13	11	27	5	4	—	60
	R	1	—	5	1	1	1	9
	MR	—	—	5	3	14	6[1]	28
	MS–S	—	—	1	—	1	7[2]	9
		Race 203						
		Ld.	**Ld.:Vc.**	**Ld.(Vc.):S.**	**Vc.**	**Vc.:S.**	**S.**	
Victoria × Landhafer	I	20	10	28	8	8	4	78
	R	—	—	3	—	—	—	3
	MS	—	—	—	—	—	2 (1 S. : Vc.)	2

[1] Four lines segregating with preponderance of susceptible plants.
[2] Three lines segregating with preponderance of susceptible plants.
For interpretation of symbols S.F., etc., see Table 8.
(Expected values in brackets.)
I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

the 114 in the class showing the necrosis associated with the Victoria reaction type and classified as having " 1n ", " 2 –n ", " 2n " or " 3n " reaction types showed segregation for the Santa Fe genotype, whilst one F_2 plant from the " 2n " to " 3n " reaction type category was homozygous susceptible. Most of these aberrant instances were those involving F_2 tests with race 203 and a closer association of reaction types between F_2 and F_3 seedlings was evident when race 226 was used in the F_2 generation.

The four plants under the F_2 " ; " reaction type category, producing susceptible progenies or segregating for Victoria type resistance and susceptibility, were almost certainly misclassifications. The discrepancies in other cases indicated that the F_2 classification was affected by modifying genetic factors or environmental variations. Further evidence for this was shown since 11 lines were homozygous resistant for the Santa Fe reaction type from F_2 plants classified as exhibiting a " 1 " or various intermediate reaction types. Later reported correlated F_3 studies involving different races produced unexpected results and, as indicated in Table 8, 28 F_2 plants out of 114 classified for the Victoria reaction type gave F_3 lines segregating for the Santa Fe factor as previously indicated.

(iv) F_2 adult plant vs. F_3 seedling

In this analysis the progenies of plants classified for adult plant reaction in the field were studied for seedling behaviour and the data are presented in Table 9.

This analysis involved tests on F_2 seedlings which had been initially classified for seedling reaction type and subsequent adult plant behaviour. In the cross Santa Fe × Landhafer three moderately resistant plants gave fully susceptible progenies. These presumably carried the recessive factor conditioning moderate resistance in the adult plant stage in Landhafer. Since these would be expected to comprise 3/64 of the population the number expected was 7·0. The probability of chance deviation was 0·2 – 0·1 for this result. Segregating progenies from the moderately resistant and moderately susceptible to susceptible classes of F_2 adult plants indicated that the single factor conditioning seedling as well as adult plant resistance in Santa Fe and/or Landhafer was incompletely dominant in the latter stage.

In the F_2 generation of the cross Santa Fe × Ukraine, the adult plant segregation conformed to a ratio of 249 resistant : 7 susceptible. Of these 249 resistant plants 64 were expected to produce homozygous resistant, 128 segregating and 57 homozygous susceptible lines. The progenies of the 58 resistant F_2 plants conformed to this hypothesis statistically, whilst two susceptible F_2 plants gave susceptible progenies as expected.

In the cross Santa Fe × Victoria, all the F_3 lines homozygous or heterozygous for the Santa Fe reaction type were expected to be derived from the resistant classes of F_2 plants. Of 63 lines of this type only one was derived from a susceptible plant and was probably an error in F_2 classification labelling. The expected ratio was one homozygous : 2 segregating progenies for this type of resistance. Twenty-five homozygous resistant lines were observed, giving a P value of 0·5 – 0·2 in the sample of 63. The remaining F_2 plants would depend for their resistance on the Victoria genes or would be susceptible. The expected behaviour of these classes in F_3 was as follows on the basis of the operation of one of the adult plant resistance factors in Victoria :

F_2 adult plant reaction	F_3 seedling behaviour (in percentages)		
	Resistant (Victoria type)	Segregating (Victoria type : susceptible)	Susceptible (including segregating with preponderance of susceptible plants)
Resistant	20·3	46·5	9·5 = 76·3
Susceptible	0·2	4·9	18·6 = 23·7
Total	20·5	51·4	28·1

Grouping together the field resistant F_2 groups (immune, resistant and moderately resistant) the observed and expected frequencies (in brackets) corresponding to the above table were as follows :

F_2 adult plant reaction	F_3 seedling behaviour		
	Resistant	Segregating	Susceptible
Resistant	9(8·7)	19(20·0)	7(4·1)
Susceptible	0(0·1)	1 (2·1)	7(8·0)

This indicated good agreement between observed and expected results.

In the cross Victoria × Landhafer, 206 F_2 plants were classified for adult plant reaction and the results are as previously set out and explained in relation to the data of Table 4. The progenies of the three resistant plants and 78 of the immune reaction class were tested. Of these 81 plants, four gave susceptible F_3 lines. From the behaviour of the Victoria genotype one-fourth of the resistant F_2 class was expected to produce susceptible F_3 lines, whilst F_3 behaviour due to the Landhafer genotype with a second factor acting solely at the adult plant stage was expected to give one-fifth of lines susceptible from the field resistant F_2 class. Hence, on combining the two genotypes one-twentieth of resistant F_2 adult plants were expected to give susceptible F_3 seedling progenies in a cross between the two varieties. The four such plants observed showed perfect agreement with the number expected.

Confirmation on the operation of the factor Vc_2 and its inhibitor was obtained since several lines in the two crosses involving Victoria showed segregation for the Victoria type of resistance with a preponderance of susceptible segregates. The behaviour of these subclasses has already been dealt with in the F_3 studies.

TABLE 10

Correlation of F_3 seedling behaviour to different races of Crown Rust in crosses involving the resistant oat variety Landhafer with certain other resistant varieties

Cross	F_3 behaviour to race	F_3 behaviour		
		Res.	Seg.	Sus. (incl. S. : Vc.)
	203	Race composite 226, 237, 237–4, 259		
Santa Fe × Landhafer	Res.	45	—	—
	Seg.	—	49	—
	Sus.	—	—	11
	226	Race composite 203, 237, 237–4, 259		
Landhafer × Trispernia	Res.	78	7	—
	Seg.	1	83	—
	Sus.	—	—	14
	203	Race composite 226, 237, 237–4		
Victoria × Landhafer	Res.	48	1	—
	Seg.	—	61	—
	Sus.(incl. S. : Vc.)	—	1	16[1]

[1] One line segregated S. : Vc. (Susceptible and Victoria reaction type plants, with susceptible types preponderant) in both tests, two segregated S. : Vc. to race composite only and one segregated S. : Vc. to race 203 only.

Seg. = Segregating, Res. = Resistant, Sus. = Susceptible

S. : Vc = Segregating for susceptible reaction type and Victoria reaction type. with preponderance of the former.

(v) F_2 seedling vs. F_3 seedling

The relationship of F_3 reactions in crosses involving Landhafer and Santa Fe are presented in Tables 10, 11 and 12. The same seedlings were tested with one race on the primary leaf and then either with a mixture of races or a second race on the secondary leaves. From Table 10 which involves data

TABLE 11

Correlation of seedling behaviour of F_3 lines to Crown Rust Race 203 and a composite of Races 226, 237, 237–4 and 259 in a cross between the resistant oat varieties Santa Fe and Trispernia

F_3 reactions to Race 203	F_3 behaviour to composite of Races: S.F.	S.F. : Tr.	Tr.
S.F.	11(10·9)	2(0·0)	—
S.F. : Tr.	13 } (12·5)	40 } (48·8)	—
Tr. : S.F.[1]	1 }	4 }	—
Tr.	— (1·6)	6(3·3)	26
χ^2 values	1·04, P = 0·7–0·5 ; 2·01, P = 0·5–0·3		

[1] Tr. : S.F. = Segregating for 1+ and ; –1 = reaction types, with the former preponderant. For interpretation of symbols S.F., etc. see Table 8.
(Expected values in brackets.)

TABLE 12

Correlation of seedling behaviour of F_3 lines to Crown Rust Race 226 and Races 237, 259 and 286 respectively in a cross between the oat varieties Santa Fe and Victoria

F_3 behaviour to Race		F_3 behaviour to Race 226: Res.	Seg.	Sus.	Total
237	Res.	59	6	—	65
	Seg.	8	69	—	77
	Sus.	—	1	22	23

F_3 behaviour to Race		S.F.[1]	S.F. : Vc.	Vc.	S.F.(Vc.) : S.	Vc. : S.	S.(incl. S. : Vc.)	Total
259	Res. (S.F.)	11	—	—	—	—	—	11
	Seg.	—	8	—	24	—	1	33
	Sus.	—	—	6	—	21	4	31
286	Res. (Vc.)	8	11	21	—	—	—	40
		(17·6)		(22·0)				
	Seg.	19	5	1	41	24	—	90
		(29·3)		(0·0)	(41·4)	(25·0)		
	Sus.[2]	15	5	—	23	1	—	44
		(16·1)		(0·0)	(22·6)	(0·0)		
	χ^2 values	2·08		—	0·011	—	—	
	P = 0·5–0·3				0·95–0·9			

[1] For interpretation of symbols S.F., etc. see Table 8.
[2] Eight lines showed S. : Vc. behaviour.
(Expected values in brackets.)
Res. = Homozygous resistant, Seg. = Segregating, Sus. = Homozygous susceptible.

relating to Landhafer crosses in such tests it was clear that there was complete agreement in reaction types in the cross Landhafer × Santa Fe. Discrepancies in the cross Landhafer × Trispernia were almost certainly due to delayed germination of some seeds in tests involving race 203. Reactions to race 203 and to the mixture of races 226, 237 and 237–4 were correlated in the cross

Victoria × Landhafer, except for two lines which were found to be segregating to the mixture of races but which were resistant and susceptible respectively to race 203. These discrepancies were probably due to errors in classification and the data indicated that the same factors conditioning seedling resistance were responsible for resistance to all the races to which both parents were resistant.

In the cross Santa Fe × Trispernia, F_3 lines were first tested to race 203 and then to a mixture of races. From the reactions presented in Table 11, 14 lines which segregated when tested with race 203 were fully resistant to the mixture of races. Similarly six lines which were homozygous for the Trispernia reaction type to race 203, gave segregating reactions to the race mixture.

Again, certain lines showed a preponderance of Trispernia reaction type plants over Santa Fe types in tests with race 203. These facts indicated the operation of certain modifying factors, which inhibited the expression of the Santa Fe gene. On the assumption of a pair of such complementary factors the expected behaviour of the F_2 Santa Fe reaction class to the mixture of races was seven homozygous lines homozygous for the Santa Fe reaction type, 8 segregating for Santa Fe and Trispernia reaction types, and one homozygous for the Trispernia reaction type. All Trispernia reaction type F_2 plants were expected to produce lines homozygous for such reaction type. The deviations were not statistically significant on this hypothesis. Minor modifications were observed in tests against the mixture of races both in F_2 and F_3 studies, since some plants in the homozygous Santa Fe lines showed " 1= " and " ; " reaction types on the same leaf.

In the cross Santa Fe × Victoria, 426 F_3 lines were tested against race 226. On the secondary leaves of 75 lines reactions to race 259, to which Victoria was susceptible, were recorded; similarly, on 174 lines reactions to race 286, to which Santa Fe was susceptible, were noted. In another test 155 lines were tested against race 237. Relationship of the reaction types in the three cases is shown in Table 12.

In tests involving races 226 and 237, to which both Santa Fe and Victoria were resistant, certain lines were resistant to one race but segregated to the other. Delayed germination, whereby certain plants escaped infection, may have been responsible for this difference. There was a general agreement in the behaviour to the two races indicating the operation for the same factors for resistance in each case except for one line which gave a segregating reaction against race 226 but a susceptible reaction to race 237, and this discrepancy was probably an error in classification. The general agreement in the reactions indicated the operation of the same factors in each variety against the two races.

In tests involving race 259 it was expected that lines homozygous for the Santa Fe reaction type would remain resistant, those segregating for the Santa Fe reaction type would segregate, whilst those of the Victoria type or susceptible to race 226 would be susceptible to race 259. There was almost complete agreement with this hypothesis except for one line, an obvious misclassification error, which was susceptible to race 226 but segregated in tests involving race 259.

In tests against race 286, from data included in Table 12, eight lines from the homozygous Santa Fe reaction type class to race 226 were homozygous resistant for the Victoria reaction type, thus clearly indicating the epistatic behaviour of the Santa Fe reaction type in this cross. On this basis the expected frequencies in the homozygous Santa Fe reaction type F_3 lines to race 226 were 20·5 per cent homozygous for the Victoria reaction type, 51·4 per cent of lines segregating for the Victoria reaction type, and 28·1 per cent of lines susceptible in tests involving race 286. All F_3 progenies showing segregation for the Santa Fe and Victoria reaction types (designated as S.F. : Vc.) in tests involving race 226 were expected to be homozygous for the Victoria reaction type (designated as Vc.) when race 286 was inoculated onto identical seedlings. From Table 12 it was obvious that the class S.F. : Vc. did not behave as expected, nor did the homozygous Santa Fe (S.F.) category, where there was an excess of susceptible lines. However, when the two classes S.F. and S.F. : Vc. were combined, good statistical agreement was obtained. Therefore the 10·3 per cent S.F. : Vc. class, giving only the Victoria reaction type, was added to the 20·5 per cent of the S.F. category to race 226 expected to behave similarly. The satisfactory agreement resulting from this procedure indicated the action of some modifying gene(s) which resulted in the expression of a reaction type resembling that characteristic of Victoria in certain lines in the S.F. : Vc. category to race 226, despite the absence of the genetic factors conditioning the Victoria type of resistance. This was also apparent since five lines susceptible to race 286 were obtained from the S.F. : Vc. class to race 226. In the other reaction classes to race 226, results from tests involving race 286 showed good agreement between observed and expected figures except for two lines, one in the Victoria reaction class and one in the category segregating for the Victoria type of resistance.

In the cross Victoria × Landhafer 114 lines were tested to both race 259 and race 286, Victoria being susceptible to the former and Landhafer to the latter race. When observed and expected results were compared on the basis of independent segregation, the chi-square value was 3·76 for four d.f., giving a P value between 0·5 and 0·3, indicating that the factors for resistance in the two varieties were independent.

Discussion and Conclusions

Segregation studies in crosses between certain members of the group of varieties comprising Landhafer, Santa Fe, Trispernia, Ukraine and Victoria, all resistant to the prevalent Australian races of crown rust, established certain facts which substantiated previous findings but provided additional information.

Firstly, the two factors in Landhafer conditioning adult plant resistance, one of which conferred seedling resistance as well, were independent of the factors in the varieties Santa Fe, Trispernia and Victoria. Indirect evidence indicated that the factors were also independent of that responsible for seedling resistance in the variety Ukraine. The reaction type of Landhafer was epistatic over those of Trispernia and Victoria.

The factor for seedling as well as adult plant resistance in Santa Fe was independent of the factors in the variety Victoria and epistatic to them. Some modifying gene(s), however, resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was allelic with the factors for seedling resistance in the varieties Ukraine and Trispernia. The factors in the three varieties were not identical, since the gene in Santa Fe conditioned resistance to a larger number of races than did the allele in Ukraine. The allele in Trispernia exhibited a higher reaction type than that in Santa Fe or Ukraine. The resistance of Santa Fe was dominant over that of Trispernia in tests against races 226, 237, 237–4 and 250 but with race 203 the Santa Fe gene was inhibited by the action of a pair of complementary factors, one contributed by each variety, which resulted in the expression of the Trispernia reaction type in the F_1 between the two varieties.

The cross between Santa Fe and Ukraine also revealed the independence of the factors for adult plant resistance in the variety Ukraine from the alleles for seedling resistance. Since the factors in the three varieties Santa Fe, Trispernia and Ukraine conditioning seedling resistance were allelic, even though segregation was not studied in crosses of Ukraine with Trispernia and Victoria, nor in the cross Trispernia × Victoria, it could be assumed from the evidence of other crosses that the factors responsible for seedling resistance in Santa Fe (as well as Trispernia and Ukraine) and Victoria were genetically independent.

The independence of the factors conditioning adult plant resistance in Landhafer and Ukraine, and the independence in turn of the Ukraine and Victoria adult plant factors, could not, however, be established in the absence of studies on the appropriate crosses.

The concept of allelism of the factors conditioning seedling resistance in the varieties indicated is proposed, although, as indicated by Luig, McWhirter and Baker (1958) with higher plants where segregating population sizes are restricted compared with microorganisms, it is technically difficult to establish closer linkage of less than a few crossover units. However, as reviewed, the hypothesis of allelism has been proposed by various North American workers, and is accepted until evidence is advanced to refute it. In this connection the fact that race 286, described by Baker and Upadhyaya (1955), and first found in low proportions on adult plants of the variety Trispernia, proved susceptible on seedlings of Trispernia, Santa Fe and Ukraine as well as Landhafer, is of interest.

F_2 seedling segregation was studied in crosses of Santa Fe with Landhafer, Ukraine and Trispernia and in the cross Landhafer × Trispernia against race 286, to which all four varieties were susceptible. No complementary gene action between these varieties was indicated since no F_2 seedling gave a resistant reaction. This also excluded the possibility of the operation of any inhibitor against this race.

These results confirmed certain conclusions proposed by Litzenberger (1949), Finkner (1954), Finkner *et al.* (1953) and Simons and Murphy (1955). More factors were, however, identified in the present instance because a larger number of races were employed in the seedling stage analyses and studies were were also made on adult plant segregation in the field.

In conformity with the symbols used in describing the factors found in Victoria (Upadhyaya and Baker, 1958), the genes for resistance revealed in the current studies are designated thus :

Landhafer—Ld_1—for adult plant resistance and seedling resistance to races 203, 226, 226–2, 230, 237, 237–4 and 259 ; —$\overline{Ld}_2$—responsible for adult plant resistance only.

Santa Fe—Sf_1—conferring adult plant resistance and seedling resistance to the same races as Ld_1 ; —Tr_a—complementary to a factor (Tr_b) in Trispernia, complementary gene action resulting in the expression of the Trispernia reaction type and inhibition of the action of Sf_1 against race 203.

Mutica Ukraine—Sf_1'—responsible for seedling resistance to races 237 and 237–4 and allelic to Sf_1 ; —$\overline{Mu}_1$—conferring adult plant resistance ; —$\overline{Mu}_a$ and $\overline{Mu}_b$—complementaty genes for adult pl nt resistance.

Trispernia—Sf_1''—allelic with Ld_1 but exhibiting a higher reaction type ; —Tr_b—complementary to Tr_a.

In the case of non-allelic genes the lower reaction type was consistently epistatic in the seedling stage.

Additional genes were revealed in certain of these varieties in crosses with Bond and will be reported in a subsequent paper.

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